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Dry matter and nitrogen accumulation and partitioning in selected soybean genotypes of different derivation

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Summary. Experiments were conducted to determine if changes in the accumulation and partitioning of dry matter (DM) and nitrogen (N) in soybean [*Glycine max* (L.) Merr.] were associated with agronomic improvements and to assess the degree of genetic variation present for these traits. Fifteen maturity group II soybean genotypes including three ancestral cultivars, three modern cultivars, and nine agronomically superior plant introductions (PI's) were grown in replicated tests at four locations in the eastern U.S. The DM and N of stems, pod walls, and seeds were determined at maturity, and the apparent harvest indices (HI) and the apparent nitrogen harvest indices (NHI) were calculated. Pod DM partitioning was calculated as the ratio of seed DM to total pod DM and pod N partitioning was the ratio of seed N to total pod N. The mean DM accumulation of the modern cultivars was significantly greater than that of the ancestral cultivars and PI's. The apparent HI and the pod DM partitioning of both the modern and ancestral cultivars were significantly higher than that of the PI's. The three modern cultivars demonstrated the highest N accumulation. As a group, the modern cultivars consistently showed maximal accumulation and partitioning of DM and N suggesting that these physiological traits are associated with agronomic improvement. No individual PI was found to possess DM or N accumulation or partitioning which significantly exceeded the best modern cultivar or ancestral cultivar, indicating that genotypes with accumulation or partitioning characteristics which exceed available germplasm may be difficult to identify. Seed yield was correlated ($P < 0.05$) with both DM ($r = 0.61$) and N ($r = 0.57$) accumulation.

Key words: *Glycine max* (L.) Merr. – Harvest index – Nitrogen harvest index – Pod partitioning

Introduction

Donald (1962) indicated that biological yield and harvest index (seed yield/biological yield) were important characteristics which could be used to improve the biological efficiency of grain crops. Similarly, the acquisition and partitioning of nitrogen (N) should be a consideration in grain crop productivity (Cregan and van Berkum 1984). In this regard, nitrogen harvest index (seed N/total plant N) has been used as a measure of N partitioning (Austin et al. 1977; Canvin 1974).

Genetic variation for dry matter (DM) accumulation and harvest index (HI) of soybean [*Glycine max* (L.) Merr.] has been reported. Hanway and Weber (1971 a) reported three distinctly different rates of dry matter accumulation among eight soybean genotypes. DM accumulation at 30 days after flowering ranged from 520 to 1,615 g/m² among a group of 34 non-nodulating soybean lines studied by Jeppson et al. (1978). Schapaugh and Wilcox (1980) observed significant differences among the HI of soybean genotypes within different maturity classifications.

Because of the stability of HI across environments, Spaeth et al. (1984) suggested HI as a predictor of soybean seed yield. However, the relationship between HI and seed yield in soybean is not well defined. Jeppson et al. (1978) reported that in each of 2 years, HI was positively correlated with seed yield. In 1 of 2 years, Schapaugh and Wilcox (1980) detected a highly significant correlation ($r = 0.91$) between HI and yield. Kenworthy and Brim (1979) used HI as a selection criterion in three cycles of recurrent selection and reported a 1.6% decrease in seed yield.

Hanway and Weber (1971 b) observed that seasonal N accumulation was similar in eight field-grown soybean genotypes. In contrast, Jeppson et al. (1978) demonstrated a range of total seasonal N accumulation among a group of non-nodulating soybean genotypes. Carter et al. (1982) compared cycles 0 and 6 of two soybean populations which had undergone recurrent selection for higher seed protein percentage. In one population, selection had increased total N accumulation in the vegetative plant parts, whereas the opposite had occurred in the second population. In the only report regarding genetic variation for nitrogen harvest index (NHI) in soybean, Jeppson et al. (1978) indicated that NHI varied from 67 to 80% among a group of seven non-nodulating soybean genotypes.

Austin et al. (1980) analyzed the DM and N accumulation and partitioning of winter wheats (*Triticum aestivum* L.) released over a 70 year period. Large yield increases in newly developed genotypes were associated with higher HI. They also indicated that while further increases in HI were possible, genetic gains in seed yield would increasingly depend upon detection and exploitation of genetic variation in biological yield. Coincident with this report by Austin et al. (1980) we undertook the current study to determine (a) if changes in the accumulation and partitioning of DM and N have been associated with agronomic improvements in soybeans and (b) the presence and degree of genetic variation in DM and N accumulation and partitioning in a group of nodulating soybean genotypes.

Materials and methods

Fifteen soybean genotypes (Table 1) including three cultivars developed by planned hybridization (subsequently referred to as modern cultivars) and released between 1947 and 1971, three ancestral cultivars which occur frequently in the pedigrees of most indeterminate cultivars grown in North America, and nine plant introductions (PI's) were used in the study described herein. The PI's were chosen from an original group of 556 obtained from R. L. Bernard (USDA, ARS, Agronomy Department, University of Illinois, Urbana, IL, USA) based upon disease reaction, vigorous growth, and single-row non-replicated yield tests at four locations. With the exception of PI 96194-3, the soybean genotypes are classified in maturity group II. Under our conditions, PI 96194-3, which is classified as maturity group III, matured similarly to maturity group II genotypes.

Field experiments were established in 1980 at four locations in the eastern U.S. including Adelphia, NJ; Landisville, PA; Clarksville, MD; and Beltsville, MD using a randomized complete block design with two replications. A plot consisted of four rows 3.6 m long with 0.76 m between rows. The planting rate was 26 seeds/m of row.

The measurement of DM accumulation of soybean is difficult because petioles and leaf blades abscise before maturity. Schapaugh and Wilcox (1980) defined apparent HI as the ratio of seed yield to mature plant weight. They reported a highly significant correlation between HI and apparent HI in each of 2 years of $r=0.96$ and $r=0.97$. In our study, all aboveground plant material was harvested from a 91 cm section of either the first or fourth row of each plot at maturity and was separated into stem, pod wall, and seed components. The quantity of DM (weight after 24 h at 100 °C) and total N in each component was determined. Total N of duplicate samples of milled dry plant tissue was determined by the Kjeldahl method (Eastin 1978 a, b). Seed yield was estimated by harvesting the two center rows of each plot which had been trimmed at maturity to 2.5 m.

Table 1. Means over locations for dry matter (DM) accumulation, apparent harvest index (HI), pod DM partitioning, and seed yield of ancestral cultivars, modern cultivars, and plant introductions

Genotype grouping and genotype	DM accumulation (g/m^2)		Apparent HI (%)		Pod DM partitioning (%)		Seed yield (kg/ha)	
Ancestral cultivars								
'Manchu'	478.9 a–d[a]		53.2 c–e		69.4 d		1,873 c	
'Mukden'	476.3 a–d		53.8 c–e		71.1 b–d		1,984 bc	
'Richland'	446.7 b–d		58.5 a		74.8 a		2,115 ab	
Mean		467.3 b[b]		55.2 a		71.8 a		1,961 b
Modern cultivars								
'Amsoy 71'	499.6 abc		58.1 ab		74.3 a		1,989 abc	
'Beeson'	518.5 ab		55.1 bc		71.5 b–d		2,274 a	
'Hawkeye'	539.6 a		53.2 c–e		70.7 b–d		2,256 ab	
Mean		519.3 a		55.5 a		72.2 a		2,173 a
Plant introduction								
PI 68522	483.1 abc		54.7 cd		72.0 bc		1,870 c	
PI 79602	460.3 a–d		50.7 ef		70.7 b–d		1,863 c	
PI 86122	454.0 a–d		51.7 ef		69.5 d		1,912 abc	
PI 96194-3	512.3 ab		47.6 g		70.3 cd		2,128 ab	
PI 297545	420.0 cd		56.4 a–c		72.9 ab		2,072 abc	
PI 360835	396.7 d		50.8 ef		69.2 d		1,787 c	
PI 361062B	495.8 abc		51.6 d–f		71.7 b–d		2,093 abc	
PI 361116	525.9 ab		49.5 fg		70.0 cd		2,071 abc	
PI 383278	476.7 a–d		54.8 cd		69.6 cd		1,949 abc	
Mean		468.4 b		52.0 b		70.6 b		1,971 b

[a] Genotype means within a column not followed by the same letter are significantly different ($P<0.05$) as tested by Duncan's Multiple Range Test

[b] Group means within a column not followed by the same letter are significantly different ($P<0.05$) as tested by planned F comparisons

Apparent HI was calculated as (seed weight/mature plant weight) × 100 and apparent NHI was determined as (total seed N/total mature plant N) × 100. Pod DM partitioning ([seed weight/(seed + pod wall weight)] × 100) and pod N partitioning ([seed N weight/(seed N + pod wall N weight)] × 100) were calculated to serve as measures of partitioning within the fruiting body.

Analyses of variance were computed for each individual location and combined over locations. Correlation coefficients were calculated for DM and N accumulation and partitioning, seed yield, and 100-seed weight using the means of the genotypes over the four locations. The six possible rank correlations for genotypic performance between the four environments were calculated for each of the DM and N accumulation and partitioning traits.

Results and discussion

Significant differences over locations were observed among the 15 genotypes for all traits except N accumulation. Significant genotype × environment interactions were present for DM accumulation, N accumulation, apparent HI, and seed yield.

Dry matter and N accumulation and partitioning

The mean DM accumulation of the three modern cultivars was about 11% greater than that of the ancestral cultivars (Table 1). Of the physiological variables measured, this difference in DM accumulation was the major distinguishing characteristic between the modern and ancestral cultivars and indicated that plant breeding for improved agronomic characteristics has also enhanced the capacity of the modern cultivars to accumulate DM as compared to the ancestral cultivars from which they were derived. We speculated that because differences in the maturity of the 15 genotypes were detected (data not shown), that differences in DM accumulation may have been related to a longer leaf area duration, thereby resulting in greater total photosynthate accumulation. The lack of correlation between days to maturity and DM accumulation ($r = -0.04$) indicated that this was probably not the case.

A significant difference in the N accumulation of the modern and ancestral cultivars was not detected (Table 2). However, of the 15 genotypes tested, the N accumulation of the modern cultivars ranked 1, 2, and 3, indicating that higher N accumulation was associated with agronomic improvement.

A substantial degree of variability for DM partitioning was present within each of the three groups of genotypes, however, both the modern and ancestral cultivar groups demonstrated a large and significant advantage

Table 2. Means over locations for nitrogen (N) accumulation, apparent nitrogen harvest index (NHI), and pod N partitioning of ancestral cultivars, modern cultivars, and plant introductions

Genotype grouping and genotype	N accumulation (g/m^2)		Apparent NHI (%)		Pod N partitioning (%)	
Ancestral cultivars						
'Manchu'	18.8 a–c[a]		93.1 ab		95.9 a–c	
'Mukden'	18.2 a–c		93.6 ab		96.1 a–c	
'Richland'	18.4 a–c		93.8 ab		96.4 a	
Mean		18.5 ab[b]		93.5 a		96.2 a
Modern cultivars						
'Amsoy 71'	19.2 a–c		93.8 ab		96.4 ab	
'Beeson'	20.0 ab		92.8 ab		95.5 bc	
'Hawkeye'	20.4 a		93.1 ab		96.2 a–c	
Mean		19.8 a		93.2 ab		96.0 a
Plant introductions						
PI 68522	17.9 a–c		92.9 ab		95.8 a–c	
PI 79602	18.3 a–c		92.3 b		95.9 a–c	
PI 86122	16.7 bc		93.1 ab		96.0 a–c	
PI 96194-3	17.9 a–c		90.3 c		95.4 c	
PI 297545	16.0 c		94.2 a		96.4 ab	
PI 360835	15.6 c		92.7 ab		95.7 a–c	
PI 361062B	18.0 a–c		92.8 ab		95.9 a–c	
PI 361116	19.0 a–c		93.2 ab		96.6 a	
PI 383278	17.4 a–c		92.8 ab		95.3 c	
Mean		17.4 b		92.7 b		95.9 a

[a] Genotype means within a column not followed by the same letter are significantly different ($P < 0.05$) as tested by Duncan's Multiple Range Test

[b] Group means within a column not followed by the same letter are significantly different ($P < 0.05$) as tested by planned F comparions

over the PI's in apparent HI and pod DM partitioning (Table 1). This finding suggested that selection for agronomic traits in the modern and ancestral cultivars had coincidently identified genotypes with desirable DM partitioning. This was not, however, true of N partitioning. The apparent NHI of the ancestral cultivars exceeded that of the PI's but the NHI of the modern cultivars did not (Table 2). The intensive selection for yield applied in the development of the modern cultivars, which increased yield and DM accumulation, may also have tended to reduce seed protein content. This is suggested by the frequently observed negative correlation between seed yield and protein content in soybean (Burton 1985). Indeed, the seed N concentration of the modern cultivars (6.4%) was significantly ($P < 0.05$) less than that of the ancestral cultivars (6.7%). Therefore, the net result of selection was little change in N partitioning.

Relationships of DM and N accumulation and partitioning and seed yield

Seed yield was correlated ($P < 0.05$) with both DM ($r = 0.61$) and N accumulation ($r = 0.57$) indicating that selection for seed yield would result in greater DM and N accumulation. However, significant genotype × environment interactions were detected for DM and N accumulation. Therefore, to accurately estimate DM and N accumulation, genotypes would have to be tested in a number of environments.

Although we had anticipated significant correlations between seed yield and apparent HI and NHI, none was detected because certain higher yielding genotypes, such as PI 96194-3 and PI 361116, had relatively low apparent HI values (Table 1). Although yield and apparent NHI were not correlated, we did, as noted earlier, find that the apparent HI of the cultivars was significantly higher than that of the PI's. Thus, while higher HI may be associated with agronomic improvement, selection for HI alone will not identify higher yielding genotypes. Nonetheless, because of the relationship of HI with agronomic improvement and reports of positive associations between yield and HI in soybean (Jeppson et al. 1978; Schapaugh and Wilcox 1980; Mullen et al. 1982; Spaeth et al. 1984), we cannot dismiss HI as a useful selection criterion. Although significant genotype × environment interaction was detected for apparent HI, the six rank correlations between the four locations were all significant and averaged $r = 0.68$. Thus, genotype × environment interaction affected the magnitude of the differences between genotypes to a greater extent than it affected the ranking of genotypes indicating that one or two environments would be sufficient to adequately assess the relative HI of soybean genotypes.

Correlation analysis detected a significant relationship between apparent HI and pod DM partitioning ($r = 0.76$, $P < 0.01$), indicating that genotypes which efficiently partitioned DM in the plant as a whole demonstrated a similar capacity within the pod. While partitioning in the plant as a whole and partitioning within the pod are related arithmetically (both have seed weight in the numerator), the correlation between apparent HI and pod DM partitioning suggests the possible use of pod partitioning in indirect selection for HI.

Although Austin et al. (1980) indicated that in winter wheat the higher productivity of modern cultivars was mainly associated with increases in HI, our data suggest that the major difference between ancestral soybean cultivars and their modern progeny was increased DM accumulation. The apparent HI and NHI of the ancestral cultivars and modern cultivars were quite similar. When compared to a group of PI's which had undergone limited selection for agronomic potential, the modern cultivars demonstrated significantly superior DM accumulation, apparent HI, pod DM partitioning, and N accumulation. In the accumulation and partitioning of DM and N, we found no instance in which the ancestral cultivar or PI group mean significantly exceeded the modern cultivar group mean. These results suggest that DM and N accumulation and partitioning are physiological traits which are positively related to the agronomic improvement of soybean. It seems likely that these traits were coincidently improved through selection for yield and other agronomic traits.

We had anticipated that the examination of a group of PI's with reasonably acceptable agronomic characteristics would allow the identification of genotypes with the ability to accumulate or partition DM or N in greater quantities or more efficiently than in currently grown cultivars. Thus, high accumulation in one accession could be genetically combined with exceptional partitioning from another. Only in the case of apparent NHI and pod N partitioning did a PI numerically exceed all the cultivars and ancestral cultivars, and in both cases the advantage of the particular PI was small. While the U.S. soybean germplasm collection includes many thousands of accessions whose DM and N accumulation and partitioning characteristics are unknown, the small sample of PI's we examined does not suggest that genotypes with accumulation and partitioning superior to those currently available are common in the collection. However, the agronomic selection imposed in choosing the PI's may have resulted in the discard of, for example, lodging susceptible genotypes with high DM and N accumulation. Similarly, genotypes which did not demonstrate vigorous growth may have been culled despite highly efficient DM or N partitioning. A better estimate of the potential variation in DM and N accumulation and partitioning would be obtained using germplasm which had not undergone previous selection for agronomic traits. The use of such genotypes in a breeding program would be complicated by their inferior agronomic potential. However, it may be initially necessary to use genotypes with inferior agronomic characteristics to develop germplasm with enhanced DM and N accumulation and partitioning.

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